The adaptive value of fungal mucous-sheaths

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Abstract: Extreme physical environments can sometimes produce unique physiological adaptations. In the forests of Monteverde, Costa Rica, many organisms are exposed to high, persistent moisture. Several species of Monteverde fungi produce fruiting bodies that are sheathed in a mucous layer. This mucous may be an adaptation to protect fruiting bodies against moisture-induced decay. As predicted by this hypothesis, the abundance of mucous-sheathed species tended to increase along the altitudinal gradient of precipitation, and very few mucous-sheathed individuals were found at low elevations. An experimental removal of mucous sheaths had no discernable effect on spore dispersal of *Calostoma cinnabarina*, but this may hav e been because the fruiting bodies were still too immature to sporulate when tested. An alternative hypothesis that mucous sheaths protect against fungivory was not supported. Mucous sheathing occured in five orders within two classes, so is clearly a pleisomorphic trait of fungi.

Key Words: Calostoma cinnabarina, *decay, elevation, fungivory, physiological adaptation*

Introduction

Selection pressures from extreme abiotic conditions can produce unusual physiological adaptations. The physical environment of Monteverde, which varies along a steep elevational gradient that influences temperature, moisture, and wind (Hartshorn 1983), provides an opportunity to explore the physiological adaptations of tropical montane species. For fungi at Monteverde and elsewhere, moisture can be a critical determinant of local and regional abundance. Most fungi require significant substrate moisture to survive, but excessive water can inhibit mycelial growth and limit reproduction by causing decay of fruiting bodies and spores (Wales 1998).

Several species of fungi at Monteverde sheath their fruiting bodies in a layer of mucous (Fig. 1), the function of which has not previously been studied. This mucous sheath could protect fruiting bodies against moisture-induced rot. If so, the abundance of mucous-sheathed fungi should increase along with altitudinal increases in precipitation (Wales 1998). Furthermore, fungal fruiting bodies whose mucous has been experimentally removed should decay quicker when exposed to water than fruiting bodies whose mucous remains intact. An alternative functional explanation for the mucous is that it protects fruiting bodies from fungivory. Under this hypothesis, mucous-sheathed fungi should show fewer signs of fungivory than sympatric species that lack mucous. Finally, mucous sheaths may not be a physiological adaptation at all. This explanation would be especially parsimonious if the presence of mucous were restricted to one phylogenetic group at Monte Verde and so could be interpreted as a synapomorphy.

Methods

We surveyed fungi in three elevation zones: low (1490 - 1650 m), mid (1650 - 1750 m), and high (1800 - 1830 m). During survey efforts lasting 2 h 45 min per elevation, we recorded the morphotype and abundance of fungal fruiting bodies within 2 m of the path. Each morphotype was scored for the presence or absence of mucous-sheaths and fungivory and identified to order using a field guide to North American mushrooms (Lincoff 1981). Surveys were conducted from 20-22 January 2000 at Monteverde, Costa Rica. We tested for relationships between elevation, fungivory, and mucous sheaths with contingency analyses.

On 21 January 2000 we experimentally removed the mucous sheaths from 4 fruiting bodies of *Calostoma cinnabarina*, a mucous-sheathed, stalked puffball, growing naturally at 1640 m. Four other fruiting bodies were left intact. All eight experimental fruiting bodies were misted (15 squirts of water) twice a day until 23 January 2000. We measured spore dispersal distance (the furthest distance spores would eject when the fruiting body was squeezed by hand), and sac wall strength (g of pressure to puncture the fungal wall with penetrometer). Treatments were compared using a Student's t-test.

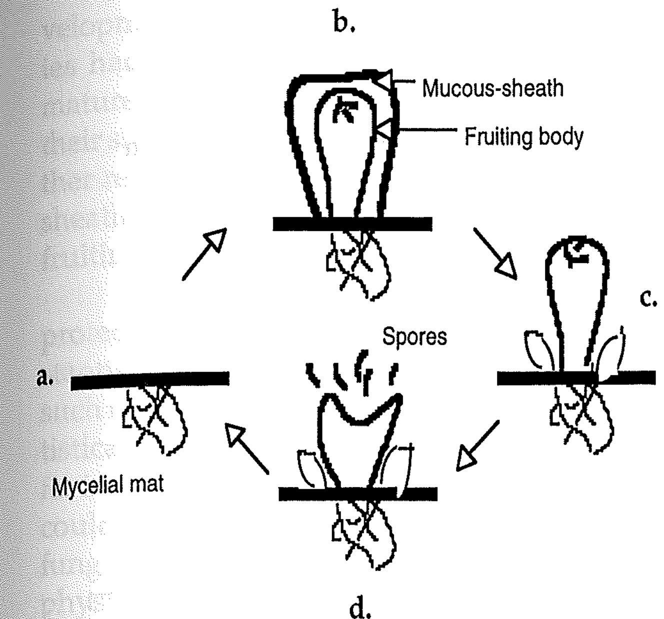

Fig. 1. Life cycle of *Calostoma cinnabarina*, a mucous-sheathed fungus. a) The fungus exists during most of its life cycle as an underground, mycelial mat. b) Given suitable environmental conditions, reproductive fruiting bodies emerge, sheathed in mucous. c) Fruiting bodies shed their mucous. d) Sporulation occurs and the remains of the fruiting bodies decay, leaving only the mycelial mat.

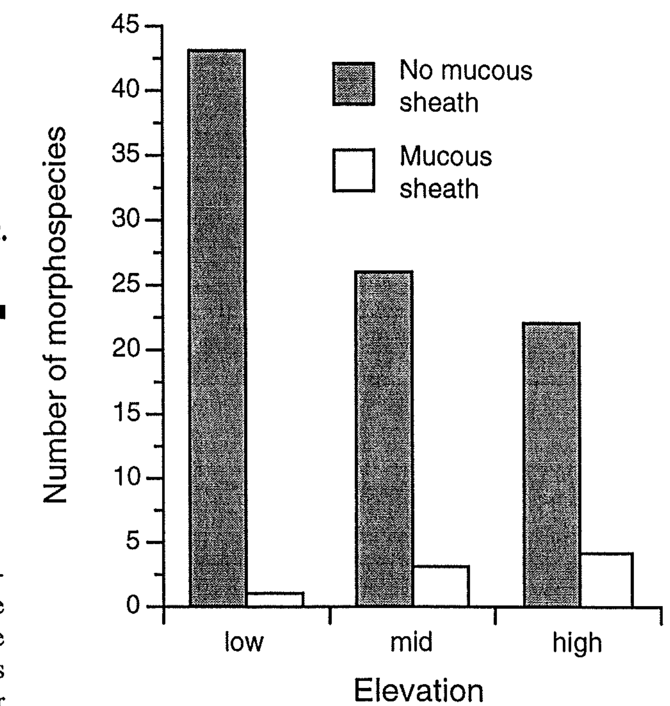

Fig. 2. Number of fruiting fungal morphospecies by elevation (with and without mucous sheaths).

Results

The number of mucous-sheathed morphospecies increased with elevation. There were twice as many mucous-sheathed species at high elevations, and only a third as many at low elevations as expected based on the hypothesis of no elevation effect (Fig. 2, G = 4.43, df = 2, p = 0.11).

The greatest abundance of mucous-sheathed fruiting bodies was found at mid elevations, followed by high, then low elevations (Fig. 3, G = 627.63, df = 2, p < 0.001). Mucous-sheathed fruiting bodies were twice the expected abundance at mid elevations, and only two-thirds the expected abundance at low elevations. We found only one mucous-sheathed fruiting body at low elevations. Mucous-sheathed morphospecies occurred within four different orders of Basidiomycetes and one order of Ascomycetes (Table 1).

Seven of 8 experimental fruiting bodies of *Calostoma cinnabarina* did not explode spores when pressured. Their spores appeared to be too immature for dispersal. There was no significant difference between sac wall strength of experimentally desheathed and sheathed individuals (mean ± SE = 55 ± 30.0 vs. 77.5 ± 33.7, respectively; $t = 0.50$, $df = 6$, $p = 0.63$).

We found no evidence that mucous protects fungi against fungivory (morphospecies with feeding damage for mucous-sheathed vs. non-sheathed = 1/12 vs. 12/102, respectively; $G = 0.14$, $df = 2$, $p = 0.71$). Fungivory tended to be somewhat lower at low elevations than at higher elevations (morphospecies with feeding damage = 2/49, 6/38, and 5/27 for low, mid, and high elevations respectively; $G = 5.20$, $df = 2$, $p = 0.08$).

Discussion

Mucous may protect fungi from excessive water saturation, as suggested by the trend for increasing mucous-sheathed morphospecies with increasing elevation (Fig. 2). Although the greatest number of mucous-sheathed morphospecies occurred at high elevations, we found more total mucous-sheathed fruiting bodies at mid elevations. Mucous sheathing was found in species representing five orders of fungi (Table 1), suggesting that it has independently evolved on several occasions (a plesiomorphy). Most fungi in the cloud forest did not have mucous sheaths; many were veiled toadstools growing in relatively dry microhabitats, suggesting there may be alternative adaptations for coping with high moisture.

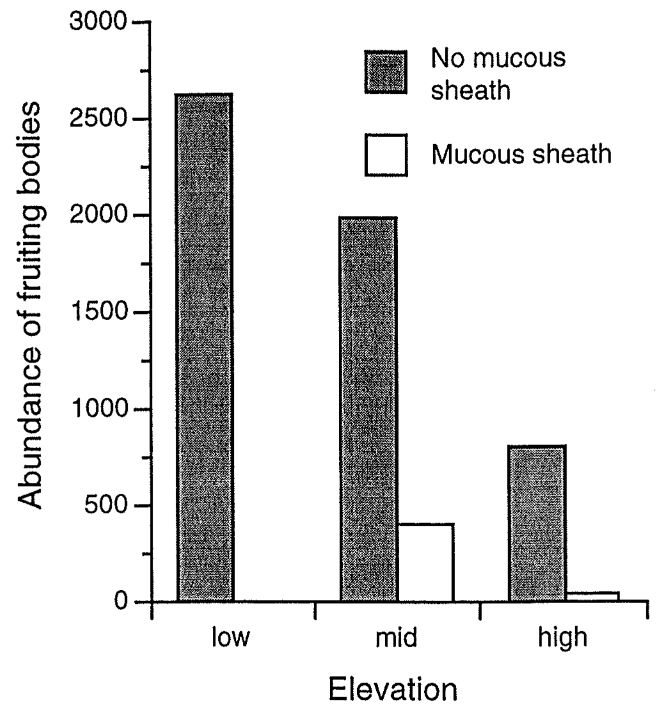

Fig. 3. Abundance of fruiting bodies by elevation (with and without mucous sheaths).

Table 1. Distribution of fungal morphospecies by elevation. Values indicate total number of morphospecies (number of mucous-sheathed morphospecies in parentheses). In addition, 2 morphospecies of slime mold (Protista) were found in low elevation and 1 morphospecies in mid elevation.

Subdivision	Order	Low Elevation	Mid Elevation	High Elevation
Ascomycete	Pezizales	2	1 (1)	1
	Sphaeriales	4	2	0
Basidiomycete	Agaricales	15 (1)	8	10 (2)
	Aphyllophorales	11	3	6 (1)
	Tremellales	9	6 (1)	2 (1)
	Tulostomatales	0	3 (1)	0

Overall, we found more fruiting bodies at mid elevations than at high elevations (Fig. 3), which is consistent with the hypothesis (Wales 1998) that high moisture limits total fungal abundance at high elevations in the cloud forest. Intermediate elevations may be favorable for fungi because there is enough soil moisture for hyphae but not so much it precludes the development of fruiting bodies and spore dispersal.

Observations during experimental manipulation of *Calostoma* suggest that mucous may be especially important in early development; the mucous sheathed fruiting bodies had undeveloped spores, while nearby mature bodies that had already naturally shed their sheaths, ejected spores successfully. Further research could explore whether mucous sheaths are a form of protection for immature fruiting bodies.

The alternative hypothesis that mucous protects against fungivory was neither substantiated nor definitively refuted. We found such minimal levels of fungivory that our statistical tests had very little power. The trend for increased mucous with increased elevation could also be explained if mucous protects fungi against cold temperature, UV radiation, physical damage resulting from wind, and desiccation. Longer, extensive manipulations of *Calostoma* would provide more robust tests for the functional significance of mucous. It remains possible that mucous sheathing is a neutral trait with no adaptive value. If mucous is a physiological adaptation to high moisture environments, then as cloud forest habitat shrinks at Monteverde due to global warming (Pounds 1999), the altitudinal distribution of mucous-sheathed fungi will probably change.

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